

STUDIES IN QUEENSLAND PANDANACEAE 1. A NEW SPECIES AND HYBRID OF *PANDANUS* L.f.

Robert Tucker

C/- Anderson Park Botanic Gardens,

Wellington Street, Mundingburra, Townsville, Qld 4812

Summary

A species of *Pandanus* section *Austrokeura*, *P. yalna* R. Tucker and intersectional hybrid, *P. × nullumiae* R. Tucker are described from Cape York Peninsula and their distribution, relationships, ecology and ethnobotany discussed.

Australia has a rich assemblage of *Pandanus* and Cape York Peninsula, the large landmass at the extreme north of Queensland is a main centre of diversity of the genus. The species there and their relationships are poorly understood. The *Pandanus* of the high rainfall region centred around Iron Range and Lockhart River Aboriginal Community on north-eastern Cape York Peninsula were the subjects of a field study conducted by me from July 1981 to July 1982.

Many of the species there were known from pistillate material only, the genus being dioecious. Prime objectives were to collect staminate material, study the ontogeny, phenology, ecology and relationships of the various species and to record whatever ethnobotanical knowledge that remained amongst the people of the Aboriginal Community.

The people at Lockhart River represent two major dialectual groups and retain much of their traditional culture, technologies and language. I soon discovered that there was a wealth of ethnobotanical information to be gathered there. The people recognise plant genera and have names for most plants and understand the properties and uses of many. During the period I stayed there the Aboriginal Community conducted their traditional men's initiation, a sort of male secret society aimed at guiding the youths into manhood. I was invited to participate, an invitation I did not hesitate to accept and was duly adopted by a family in the community, so as to have the relatives necessary for the initiation process. The various relatives proved to be of great value, particularly with advice on *Pandanus* locations, distributions, technologies and terms. One relative from the 'Ngachi-kincha' (bora-law, = initiation process and its complex laws) is honoured in the name of the new hybrid described herein.

Ongoing studies into the ontogeny of the Lockhart River *Pandanus* are being conducted with live material cultivated in the indigenous-species Pandanetum at Anderson Park Botanic Gardens in Townsville, to augment data recorded in the field. Such data include that gained from the dissection of entire caulomeres (leaf-crowns) to better understand the sequence of leaf modification within the growth cycles. Due to the rhythmic terminal flowering the leaves are reduced to become bracts on the inflorescence peduncle with a new axillary shoot forming, firstly with prophylls, then leaves and finally flowering again. The position of the leaves on the caulomere relative to the peduncle can greatly influence leaf form and is a major consideration when studying herbarium material.

Staminate material was collected of all species present including one described herein. Certain insect pollinators were collected and records and collections made of numerous associated plants. The bulk of the material is at QRS with some duplicates at BRI and KLU.

Several important observations regarding *Pandanus* ontogeny and phenology were made and will be discussed below, however one may be briefly dealt with here. Some authors, particularly Stone (pers. comm.), have noted that many species of *Pandanus* display sexual dimorphism in the extent of branching. Male trees are often more richly branched than females, the reason for this being unclear but a possible higher frequency of flowering in males (e.g. more opportunity to branch) is implied. From my observations it seems that female and male trees generally flower synchronously only once annually and that females are often carrying mature fruit when the next flowering begins. Possibly,

in terms of biomass production, the females cannot afford the rich vegetative growth of the males which produce comparatively small and ephemeral flowers. It is also possible that having fewer branches is advantageous for seed production; *Pandanus* has no ability to enlarge the stem diameter with added branching, hence additional branches become smaller and unable to support large fruits with a high carpel number. Richly branched females may be able to produce many fruit but the reproductive potential would probably be greatly reduced as carpel number per syncarp and seed size were reduced.

Pandanus generally are not closely comparable to other monocotyledonous trees and present certain problems when their structures are studied. It is often difficult to find suitable terms for some of their parts; however, an attempt has been made here to use those which are now somewhat standardised. For convenience a few important terms are listed as follows:

- prop-root –any above-ground primary root
- pneumatophore –specialised secondary roots growing vertically from primary roots above and below ground allowing gaseous exchange
- stolon –any creeping and rooting axillary shoot being a means of vegetative propagation
- phalange –a group of united carpels within the syncarp
- staminal phalange –a group of stamens united on a common filament

***Pandanus yalna* R. Tucker, sp. nov.** affinis *P. solms-laubachii* Warb. a quo distinguitur foliis latioribus nitidioribus, pericarpio eduli flavo et phalangibus apicalibus instructus pluribus carpellis. **Typus:** Cook District: Tozer's Gap, 22 Jan 1982, *Tucker 328* (pistillate) (holotypus QRS).

Trees erect, 10–(20) m high, much branched above, branches alternate or whorled. Trunk to 8 m high, 40–100 cm basal diam., with few to many stolons, prop-roots few to numerous, 100 cm × 3 cm, densely clothed with numerous erect, adventitious rootlets at the base, those on the roots become functional pneumatophores up to 40 cm high. Bark greyish-brown, leaf-scars indistinct. Branches semi-erect, ascending to 10 m, bark greyish-brown, fissured, leaf-scars conspicuous, each bearing an adventitious axillary shoot to 4 mm diam. Leaves in the terminal rosettes semi-erect, arching from the base, bending midway, on juveniles to 3 m × 10 cm, adults usually narrower and shorter to 2 m × 6–8 cm, linear, acuminate with a fine subulate apex, coriaceous, margins and abaxial midrib dentate, upper surface semi-glossy mid-green, paler and semi-glaucous beneath with a glossy brown area at the base. The base with a shallow, rounded keel, margins entire for 13 cm from base, above which the prickles antrorse, 1–3 mm long, 1 cm apart, white with a darker greenish-brown tip, the midrib beneath unarmed. At mid-section the leaf has a shallow, usually asymmetric keel, the laminas ± drooping towards the margins where the antrorse prickles 1–2 mm long, 5–10 mm apart, the midrib beneath with a few scattered prickles 1–3 mm long, 5–10 mm apart, all antrorse or rarely a few retrorse. Towards the apex the leaf with a shallow keel, the margins ascending with antrorse prickles 1 mm long, 1–4 mm apart, prickles on midrib below similar and becoming smaller and closer towards the apex. Syncarp terminal, horizontal or rarely semi-pendulous, pedunculate, bracteate, ovoid-spherical, subtrigonal, to 25 cm × 21 cm, phalanges 110–127, multicarpellate. Peduncle to 20 cm × 25 mm, trigonous with ± 9 bracts, the lowermost green, foliaceous, to 127 cm long, the uppermost dry, variously eroded, black or brown. Phalanges with 10–31 carpels, highest numbers usually near apex, 55–60 mm × 15–50 mm, tapered towards the base, the apex ± truncate, widest point 10–15 mm from apex, the upper surfaces papillose, the lower surfaces ± smooth, the whole with numerous longitudinal, angular sulci extending from just below the carpel apex to just above the base. Carpel apices conic-pyramidal, to 10 mm high, the peripheral carpels with variously flattened apices. Stigmas vertical to oblique, linear to caudate, dark brown to black. When ripe the upper part of phalange dark orange to brown, the lower portion bright yellow to orange-yellow. Pericarp fibrous, the upper part vaulted, the fibred embedded in a mass of spongy aerenchyma, the lower part succulent and edible. Endocarp median, dark brown, bony. Seeds median, cylindrical with tapered ends, 10–22 mm × 1.5–2 mm, white, edible. Staminate inflorescence terminal, semi-pendulous, often supported by the leaves, pedunculate, bracteate, to 100 cm long. Peduncle 10–16 cm × 15 mm, white, trigonous. Rachis to 52 cm long, with tristichous ranks of 24–30 bracts, each subtending a staminate branch, the lowermost bracts to 175 cm long,

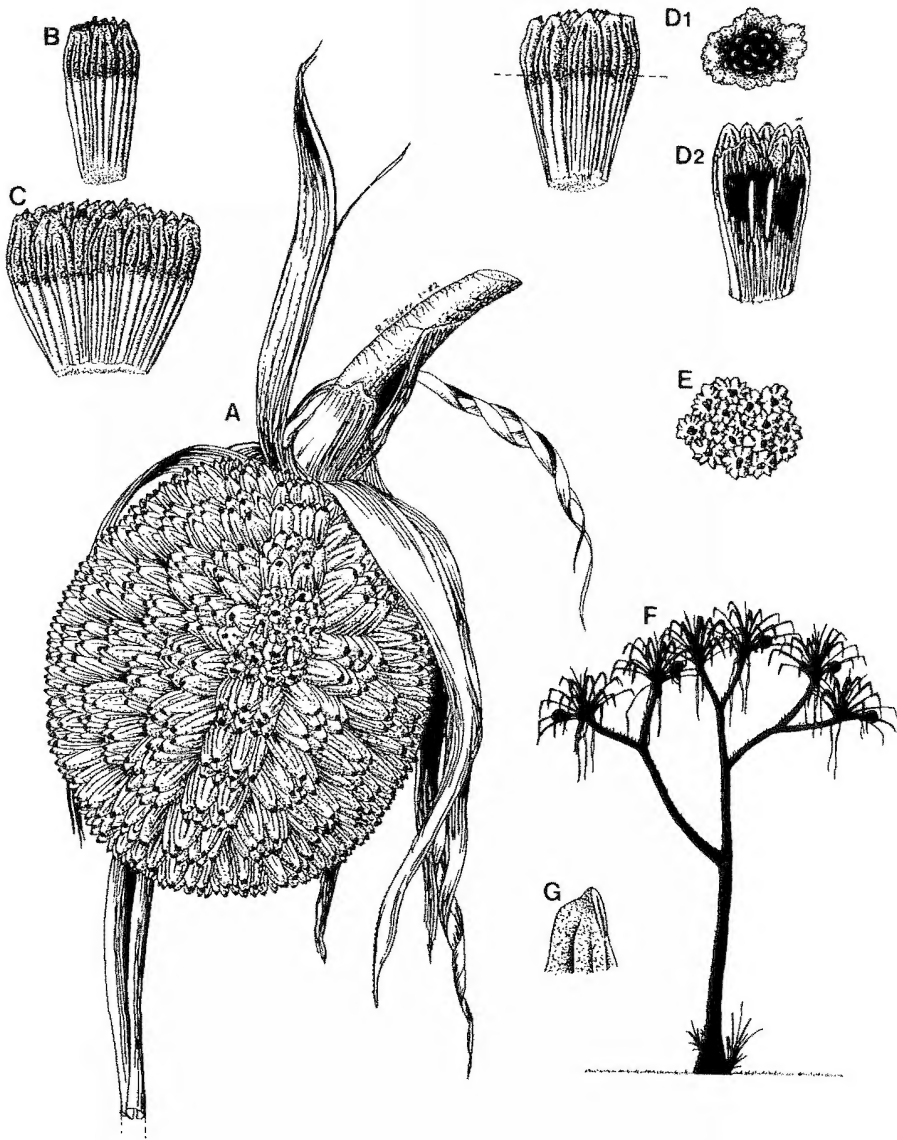


Fig. 1. *Pandanus yalna*: A. syncarp $\times 1/4$. B. few-carpellate phalange $\times 1/2$. C. multicarpellate phalange $\times 1/2$. D1, phalange in transverse section $\times 1/2$; D2, phalange in longitudinal section $\times 1/2$. E. phalange from above $\times 1/2$. F. carpel apex and stigma $\times 21/2$. G. habit of pistillate tree $\times 1/100$.

finely dentate along margins and midrib, white, soft, caducous, decreasing in length and width towards inflorescence apex. Staminal branches to 12 cm long, with numerous staminal phalanges to 25 mm long, those near the rachis longest, a few with a narrow bracteole to 25 mm × 3 mm, minutely dentate along the margins. Stamens numerous, filaments 4 mm × 1 mm, anthers 5–6 mm long, terminated by a fine apiculus to 1 mm long. **Figs 1–3.**

Distribution: North-eastern Cape York Peninsula, on the coastal lowlands and ranges to the western slopes of the Great Dividing Ra. to at least 350 m alt., from just south of Coen (14°10'S, 143°14'E) to the Dulhunty River (11°49'S, 142°29'E) with a small outlying occurrence near Batavia Landing (12°11'S, 141°56'E) on the lower reaches of the Wenlock River in north-western Cape York Peninsula.

Queensland. COOK DISTRICT: Tozer's Gap, 22 Jan 1982, *Tucker 327* (staminate) (BRI, QRS); same location & date, *Tucker 328* (holotype) (QRS).

Etymology: The specific epithet comes from the Lockhart River Kuuku-ya'u and Uutalnganu dialects names for this plant: 'Yaln-a'.

Relationships: *P. yalna* is closely related to *P. solms-laubachii* the type of *Pandanus* section and series *Austrokeura*. Section *Austrokeura* B. Stone as circumscribed by Stone (1978) is represented in Australia by the series *Austrokeura* B. Stone and *Spirales* B. Stone, which he considered had two morphological and geographical/environmental extremes. Differences between the series are summarised in **Table 1.**

Table 1. Comparison of series *Austrokeura* and *Spirales*.

	<i>Austrokeura</i>	<i>Spirales</i>
adult leaf dentation	± dentate throughout	± entire
phalange	elongate, many carpels, sulcate, red to yellow	rotund, few carpels, ± smooth, reddish
carpel apex	pyramidal	oblate to low conic
distribution	eastern Queensland	western Cape York Peninsula, N.T. & northern W.A.
habitat	moist savanna to swampforest	seasonally dry savanna

Intermediates between the series do occur particularly in areas that combine dry savanna and permanently moist swamps and swamp forest, as in parts of eastern coastal Queensland, Cape York Peninsula and the northern Northern Territory. Stone (1978) suggests a possible 'hybrid belt' bridging the two series, so great is the mixing of characteristics in some regions. Generally, however, there is a conspicuous conformity to the morphology of the series within their respective regions. Section *Austrokeura* occurs over most of northern Australia and extends into New Guinea and nearby Moluccan islands.

P. solms-laubachii occurs on the coastal lowlands and ranges from about Ingham (18° 45'S, 146° 10'E) to Cooktown (15° 20'S, 145° 10'E) and extends on to the lower tablelands to at least 600 m alt. It is variable and numerous described species have been referred to it (Stone, 1974). Some combine features of series *Spirales*; for example, red pericarp, low conic carpel-apices, reduced carpel number and variable adult leaf dentation ranging from partially entire throughout to entire on one margin. It is frequently found growing in open sites along seasonal watercourses and rarely in deep, permanent water. The leaves tend to be somewhat glaucous, straight and not arching, the pericarp hardly edible and basal stolons variable but sometimes up to 10 m long.

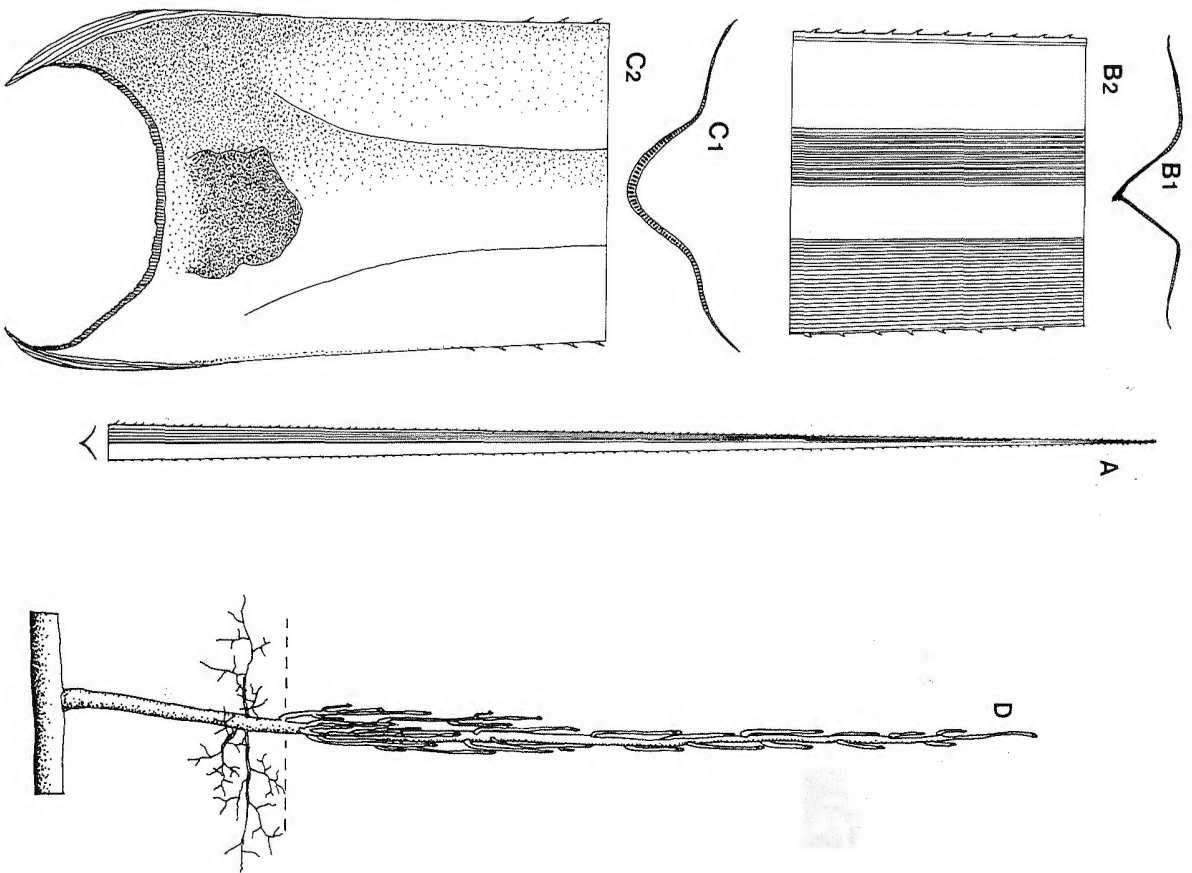


Fig. 2. *Pandanus yahnai*: Pistillate leaf. A, leaf apex and transverse section $\times 1/2$. B, leaf mid-region $\times 1/2$: B1, in transverse section; B2, from above. C, leaf base $\times 1/2$: C1, in transverse section; C2, from above. D, pneumatophore $\times 1/3$.

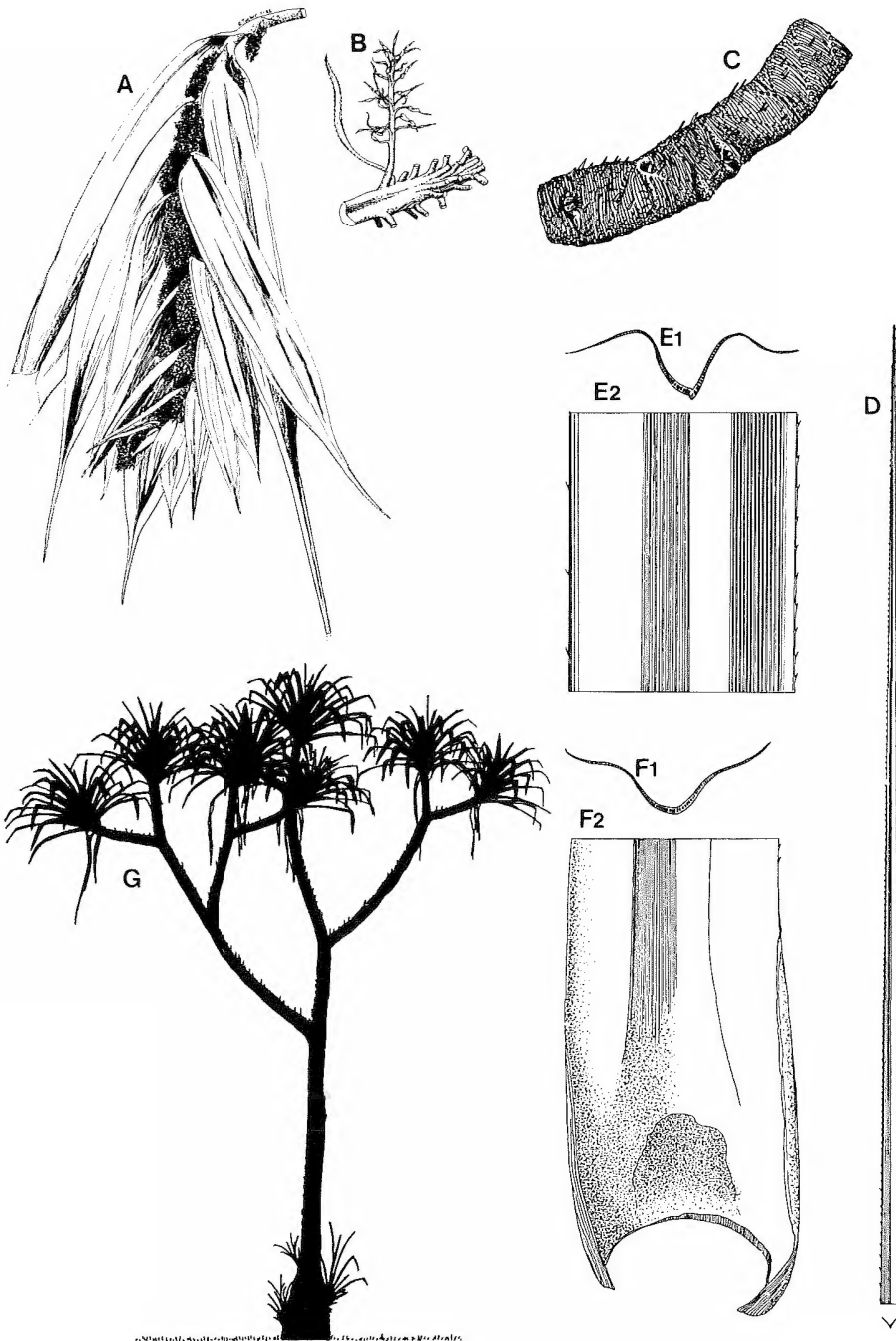


Fig. 3. *Pandanus yalna*: Staminate plant. A. inflorescence $\times 1/6$. B. branch with bracteole and phalange $\times 1$. C. detail of branch $\times 1/6$. D. leaf apex and transverse section $\times 1/3$. E. leaf mid-region $\times 1/3$; E1 transverse section; E2, from above. F. leaf base $\times 1/3$; F1, transverse section; F2, from above. G. habit of tree $\times 1/60$.

By contrast *P. yalna* is uniform throughout its range, has arching, broader, glossier leaves and edible yellow to orange-yellow pericarp. It always grows in sites which are permanently moist or wet, sometimes in very deep water (to 1.5 m) which becomes rather acidic at the end of the dry season. Vegetation types range from sedge/fern swamps through to broadleaf swampforest, riverine gallery forests and mangrove margins, rarely littoral strand around freshwater soaks, rainforest and (brackish) mangroves. This species also displays a higher degree of sexual dimorphism than does *P. solms-laubachii*. The males are often shorter and more richly branched, the branches being equal axillary pairs, resembling dichotomies, whereas in *P. solms-laubachii* it is mostly difficult to distinguish the sexes without fruit or inflorescence evidence.

P. yalna juveniles often produce leafy stolons from the lower axillary buds, particularly when growing in deep water in an open situation. These stolons grow down to the soil/water level and become repent for up to 2 m, then grow into trees similar to, but often larger than, the parent. In shady sites the trees can grow to 20 m and are usually single-stemmed, although they produce a few leafy shoots on the lower 3 m of trunk. Figs 1G, 3G. With its semi-glossy, broad and arching leaves and preference for shaded, wet sites, *P. yalna* is unique amongst members of section *Austrokeura* and appears to be primitive, its relatives being, for the most part, well adapted to life in seasonal savannas where they tolerate regular burning and droughts. Such a habitat is possibly only recently exploited by *Pandanus*, the bulk of species of which are rainforest plants.

The fruits are distributed by water and various animals (flying-foxes, birds, rats, etc.) and the pollen is insect distributed with wind playing a doubtful role. The trees generally grow in such sheltered situations that air movement around the leaf crowns sufficient to carry pollen to adjacent females would be greatly limited. At anthesis the inflorescences are distinctly hot and produce a strong scent. Inflorescence temperature elevation and its bearing on scent production and pollination in *Pandanus* is a new area of study and more detailed mention will be made of it in a separate section below.

Ethnobotany: In the Lockhart River region *P. yalna* is abundant and was formerly of some importance to the local Aboriginal people. Here all *Pandanus* come under the generic name "Tangka" and each has a particular name. The 'maii' (fruits) of 'Yalna' were eagerly sought when ripe, the older people recruiting young boys to climb the tall trees. The fruit and entire leaf-crown were harvested. The soft basal part of the pericarp was eaten raw, having little calcium oxalate, unlike fruits of other species of section *Austrokeura*. The tender growing point and young leaves were eaten raw, being similar to palm 'cabbage'. The fruits have an unusual scent, like soap and ripe pineapple together, but the taste is far from unpleasant, being more like oily pineapple with a very faint suggestion of starch.

The leaves are still occasionally harvested and after removal of the 'aka' (marginal prickles and midrib) are cut into thin strips, dried and woven to make the 'urrkutu', a headband worn by the young men during the final ceremony of their initiation. *P. zea* St. John ('Kaku-lamu') is the preferred species for this purpose but the leaves of *P. yalna* are used when the former is unavailable.

In October 1980 I observed a very distinctive and handsome *Pandanus* growing near Wachi (creek) in the Lockhart River Aboriginal Reserve (12° 49'S, 143° 20'E). This tree, although sterile, exhibited characteristics of sections *Austrokeura* and *Australibrassia* St. John. It was revisited in August 1981, and another similar tree located nearby. Another sterile tree was located 20 km away at Quintel Beach (12° 48'S, 143° 30'E) in December 1981. In May a fertile pistillate tree of this taxon was discovered near the Lockhart River Aboriginal Community. Its fruit morphology was intermediate between that of the putative parental sections. It is here named *P. × nullumiae* R. Tucker. It is the first hybrid in the genus to be formally described.

The recognition of an intersectional hybrid raises the question as to whether or not the putative parental sections deserve sectional as opposed to subsectional status. *Austrokeura* was raised to its present position from subsectional level within *Pandanus* on the basis of the distinctive morphology of this group (Stone 1978) while *Australibrassia* was originally afforded sectional status within a totally different infrageneric classification

system (St John 1960). However, recent field studies have indicated that section *Australibrassia* is not clearly defined. I expect further studies will support the reduction of *Austrokeura* and *Australibrassia* to subsectional level within section *Pandanus*.

Pandanus* × *nullumiae R. Tucker, hybrida naturalis inter *P. yalna* R. Tucker et *P. conicum* St. John ab illo statura parviore, paucioribus radicellis in trunco et radicibus et ramis, foliis angustioribus, syncarpio pendulo, phalangibus paucioribus et seminibus paucioribus sed latoribus, a hoc amplioribus, pluribus longioribus erectis radicellis in trunco et radicibus et ramis, latoribus pallentibus phalangibus pluribus paginis sulcatis et seminis angustioribus differt. **Typus:** COOK DISTRICT: Lockhart River Aboriginal Reserve, Unchi Creek, 19 May 1982, *Tucker* 376 (holotypus QRS).

Trees erect or leaning, 8(-10) m high, little to much branched above, branches whorled. Trunk 4 m × 20 cm, rarely with a few adventitious stolons near the base, prop-roots few to numerous, 35 cm × 3-5 cm, with longitudinal rows of short prickle-like to erect, linear adventitious rootlets, bark grey to brown with scattered erect rootlets, leaf-scars indistinct. Branches spreading to ascending, to 6 m long, bark tan-brown to grey, leaf-scars conspicuous, each bearing an axillary adventitious shoot 3-4 mm diam. Leaves in terminal rosettes, to 2 m × 5 cm, arching from the base, bent about midway, linear, acuminate with a fine subulate apex, coriaceous, margins and midrib beneath dentate, upper surface semi-glossy mid-green, paler and semi-glaucous beneath with a pale brown area at base, the base with a shallow keel, 75 mm wide, margins ascending, basal 5-12 cm entire, then with antrorse prickles 1-2 mm long, 7-10 mm apart, at midway the leaf with a shallow keel, asymmetric, 5 cm wide, the laminas ± drooping towards the margins where the antrorse prickles 1-2 mm long, 7-15 mm apart, a few retrorse, 30 cm below the apex, the leaf 1 cm wide, keeled, margins and midrib with antrorse prickles 0.5-1 mm long, 2-4 mm apart. Syncarp terminal, pendulous, pedunculate, bracteate, spherical, 17 cm diam., phalanges 65, multicarpellate. Peduncle 30 cm × 2 cm, trigonous, bracts to 35 cm long, eroded, dry, dark brown to black. Phalanges 40-50 mm × 25-35 mm, widest about the middle, base and apex ± truncate, in cross-section ± hexagonal, carpels 5-15, minutely papillose above, smooth below, the whole with numerous shallow longitudinal sulci. Carpel apices pyramidal, stigma terminal, horizontal to oblique, linear to circular, 1.5-2 mm long. Pericarp fibrous, lower part succulent, endocarp median, dark brown, bony, seeds median, fusiform to cylindrical, 10-15 mm × 3-4 mm. Receptacle ovoid, 75 mm long, with acute apiculum. Male inflorescence unknown. **Figs 4 & 5.**

Distribution: The hybrid is known from only three locations, all within the Lockhart River Aboriginal Reserve. However, it is expected that further locations will be discovered in the vicinity of Lockhart River and perhaps other parts of north-eastern Cape York Peninsula.

Etymology; The epithet of the hybrid honours Mrs Nullum Marrott, of Lockhart River Aboriginal Community, custodian of the women's ceremonial culture (in particular the women's dances performed during initiation rites) for her support as 'Paapa-muka' (ceremonial and substitute mother) during my initiation and for her advice regarding *Pandanus* locations.

That *P. × nullumiae* is a hybrid between *P. yalna* and *P. conicus* is indicated by its intermediate morphology and association with the putative parents, a comparison of which is summarised in **Table 2.**

P. conicus is a widespread, variable species occurring over much of the range of *P. yalna* from its southern limit extending north to Cape York. It is common and gregarious in littoral closed forests, brackish riverine gallery forests, on mangrove margins, and in almost any situation that excludes highly competitive climbers such as *Calamus*. Because of this wide ecological amplitude it is frequently associated with other species of *Pandanus*. It does not occur, however, in dense rainforest, on sites subjected to regular burning, and in open swamps and deep water. Because it is absent from water, it rarely forms an association with *P. yalna*. In the few locations where it has been observed with *P. yalna* it occurs in rather broad ecotones between gallery forest and semi-deciduous vine forest, swampforest and littoral closed forests and between gallery forest and heath.

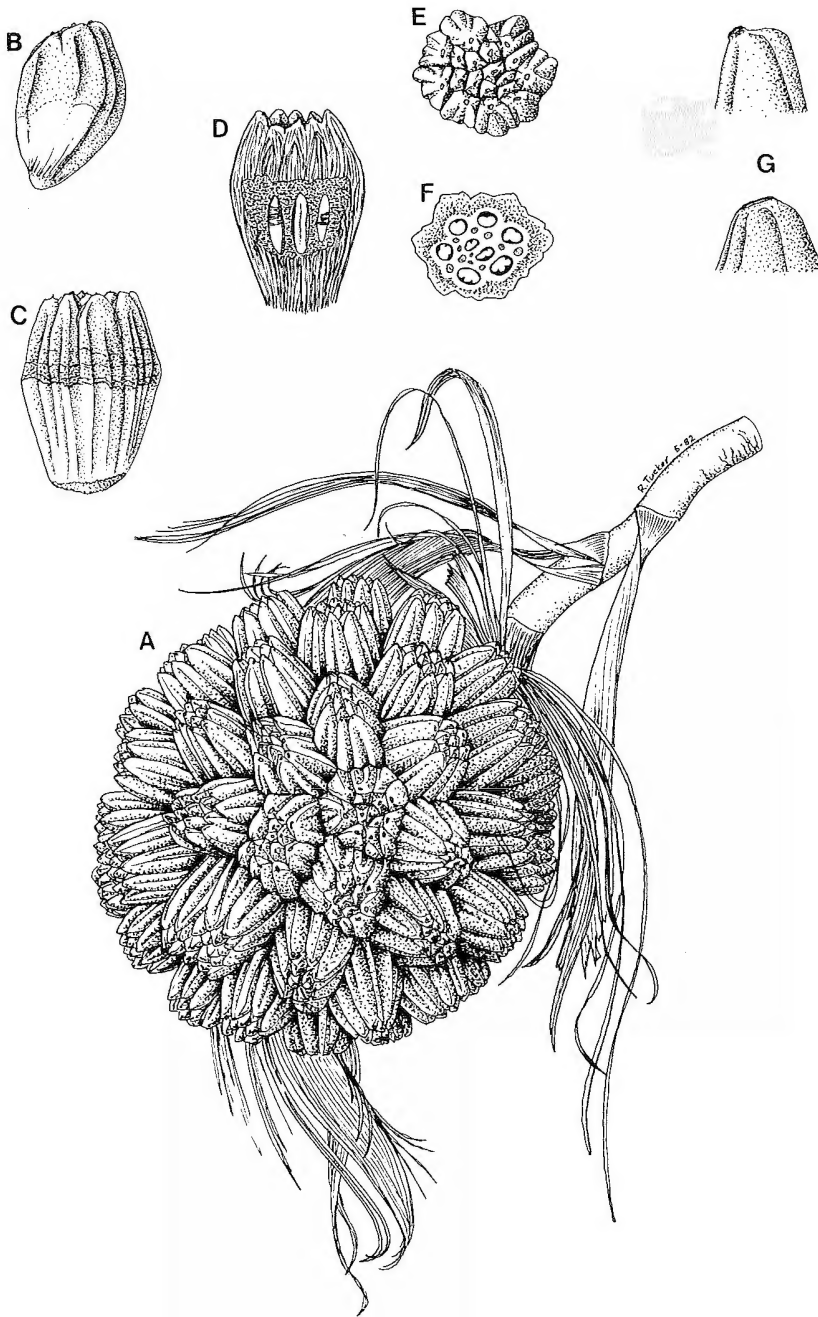


Fig. 4. *Pandanus x nullumiae*: A. syncarp $\times 1/3$. B. basal phalange. C. median phalange $\times 1/2$. D. phalange in longitudinal section $\times 1/2$. E. phalange from above $\times 1/2$. F. phalange in median transverse section $\times 1/2$. G. carpel apices and stigmas $\times 3$.

Table 2. Comparison of *P. yalna*, *P. × nullumiae* and *P. conicus*.

	<i>P. yalna</i>	<i>P. × nullumiae</i>	<i>P. conicus</i>
leaf colour	mid-green	mid-green	dark to mid-green
leaf length/breadth ratio	1:27	1:40	1:56
syncarp habit	horizontal	pendulous	pendulous
phalange no.	110-127	65	± 20
apex	papillose, broad	minutely papillose, gathered	smooth, crowded
stigma	vertical to oblique	oblique to horizontal	verticle to horizontal
seed	cylindric, ends tapered, 10-22 mm × 1.5-2 mm	fusiform cylindric, 10-15 mm × 3-4 mm	ovoid, 10-15 mm × 5-7 mm
receptacle apex	truncate	acute	acuminate

Because of the long peduncle, as in *P. conicus*, the syncarp of *P. × nullumiae* hangs below the leaves. In *P. yalna* the peduncle is short, so the syncarp is supported by the leaves. The peduncle of *P. conicus* is disproportionately long compared to other species of subgenus *Pandanus* in Australia.

The short adventitious rootlets on the prop-roots, trunk and branches of various species of subgenus *Pandanus* are distinctive enough to be of diagnostic importance at sectional level. Species of section *Austrokeura* usually have erect, narrow and rather pliable rootlets in varying densities, depending on environment and age of the tree. Trees at very wet sites or in high rainfall zones often have extremely dense and long rootlets. These often form in the axils of extant leaves and can grow through the bases as the leaves die and decay, preventing the fibrous remains of the leaves from falling away entirely. This results in the 'shaggy' appearance of *P. yalna*, especially when this covering is colonised by epiphytes. In members of section *Australibrassia* the rootlets are usually short and conical with extremely pungent apices, functioning more like prickles and apparently not adapted to gas exchange or moisture intake as in members of sections *Austrokeura* Fig. 2.

In *P. × nullumiae* the adventitious rootlets are intermediate in form between these types, being somewhat erect but short and hard, with expanded or bulbous bases. A few may approach either parental type but most are intermediate. A small amount of leaf fibre may persist on the lower trunk, held in place by the adventitious rootlets, but the trunk is generally clear of such material and as a result is usually free of epiphytes.

Hybridity: Hybrids of *Pandanus* have not been formally described previously and little has been mentioned on the subject in the literature (Stone 1976, 1982a). It appears that most pandan-rich areas contain species which retain their genetic integrity through barriers such as ecological isolation and differences in flowering time. However, north-eastern Cape York Peninsula offers much potential for hybridisation.

In general the topography is varied but with an extremely narrow altitudinal range and the climate is relatively uniform. Most species are confined to particular habitats but it is always possible to find certain locations which accommodate a number of species together and then they are usually from different subgenera. Of the three subgenera present in the Lockhart River area, subgenus *Pandanus* is the only one with more than one species.

The potential for hybridisation between various species of *Pandanus* in the Lockhart River area was clearly evident. Prior to my stay there, the staminate plants of all species except *P. zea* (subgenus *Lophostigma*) and *P. tectorius* Parkinson ex Z. (subgenus *Pandanus*) and their flowering times were unknown. Beginning in December

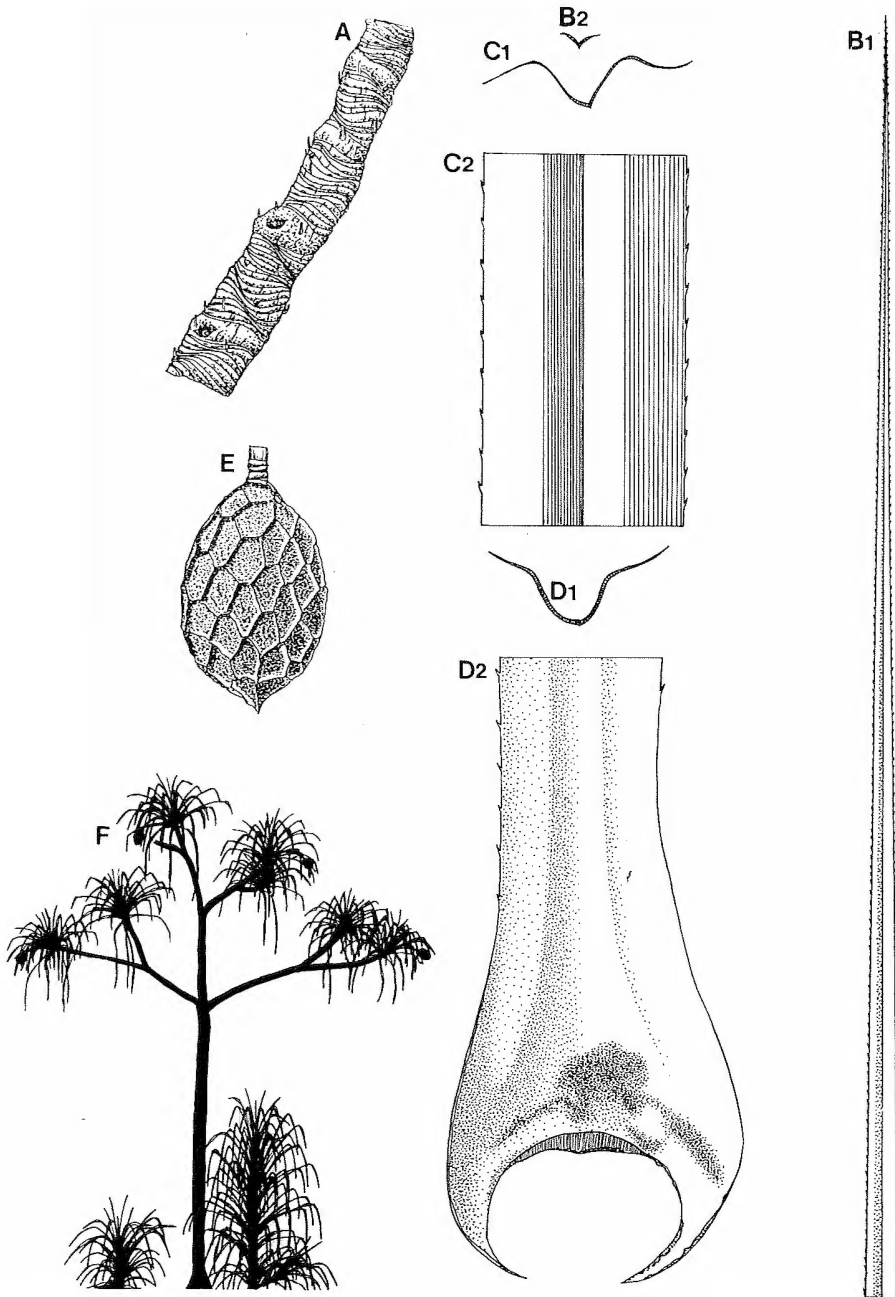


Fig. 5. *Pandanus* × *nullumiae*. A. detail branch × 1/6. B. leaf apex × 1/2; B1, from above; B2, transverse section. C. leaf mid-region × 1/2; C1, transverse section; C2, from above. D. leaf-base × 1/2; D1, transverse section; D2, from above. E. receptacle × 1/3. F. habit of pistillate trees × 1/140.

1981, various populations in the area around Lockhart River were monitored until flowering began. All species of subgenus *Pandanus* flowered synchronously over a four week period, commencing in late January 1982, although *P. tectorius* flowered from December to March it peaked during the same few weeks.

Very little is known of the phenology of the genus as a whole, but observations of wild plants indicate that a single, short flowering period during the rainy season is common, at least to species in subgenus *Pandanus*. Cultivated plants behave somewhat differently and are probably unreliable as indicators of the flowering cycles of their wild counterparts, particularly when conditions diminish the effect of climatic seasonality.

Whilst observing and collecting staminate and pistillate inflorescences, particularly those at anthesis, I discovered various insects which are possible pollen vectors. These insects were present on the staminate inflorescences of all *Pandanus* species (regardless of subgenus or section) in the study area. They include native and introduced bees, large Scarabid beetles and small Nitidulid beetles. Some of these were collected for positive determination. Of these only the Nitidulid beetles were frequent on flowering syncarps.

There is scant information about pollinators of *Pandanus*. It has been assumed that wind plays an important role in the pollination of species from exposed habitats, such as savanna, along river banks and on the littoral strand (Stone 1982b). Evidence obtained at Lockhart River during the course of the study indicates that such wind pollination may not be the case at all. All *Pandanus* species were found to have some degree of temperature elevation of the staminate inflorescence, both staminate and pistillate inflorescences emitted strong and similar scents and pistillate inflorescences exhibited nectar secretion in minute quantities on and around the stigmas. *P. tectorius*, a species of the littoral strand and dunes, exhibited inflorescence temperature elevation, scent emission and nectar secretion on both staminate and pistillate inflorescences.

Inflorescence temperature elevation has been recorded in certain families, notably Areaceae and Araceae, and is thought to be related to stages of floral development and perhaps pollen shedding and stigmatic receptivity (Schroeder 1978), whilst scent and nectar production are doubtlessly adaptations to faunal pollinators. Possibly, inflorescence temperature elevation is a means of dispersing scents derived from volatile essential oils produced prior to and during anthesis. Some species are rich in such oils and are tended and cultivated in some countries as a source of perfume. In India there exists a locally important industry based on cultivars of *P. odoratissimus* L.f. (subgenus *Pandanus*), a species which is closely related to, and in some ways difficult to separate from, *P. tectorius*. The inflorescences are gathered from cultivated male trees and the essential oil extracted as a perfume base (Purseglove 1972).

Unfortunately I had not anticipated the temperature elevation of *Pandanus* inflorescences and had no means of measuring it in the field. The temperature of staminate inflorescences of *P. tectorius*, in one instance, continued to rise after they were collected and treated with alcohol as a preservative, to the extent that I thought they might cook themselves. Perhaps the high temperature of the specimens was caused by their treatment. In any case I was alarmed at the heat generated inside the package of duplicates and unpacked them in attempt to cool them down. The chemistry and mechanics involved with this phenomenon warrant further study.

During the peak flowering period of *Pandanus* at Lockhart River, the absence of wind was noticeable. At this time of the year (January to late February) the north-west monsoon was entrenched and the Great Divide acted as a barrier to air movement from interior parts of Cape York Peninsula. By contrast the dry-season (south-east monsoon) commencing every May or June and lasting until December, is a time of constant south-east winds and almost no flower production amongst the *Pandanus* populations. From the available evidence it seems that the Lockhart River *Pandanus* are adapted to faunal pollinators during a period when wind (as a pollen dispersal agent) would be unreliable. There is no reason to suppose that Lockhart River is unique in this way, but knowledge of *Pandanus* phenology and pollination in most other parts occupied by the genus is lacking or at best very poor and will require much field work to remedy.

Allowing for the factors outlined above, it is odd that hybrid *Pandanus* are not more abundant on north-eastern Cape York Peninsula. However, the narrow ecological amplitude of some species is probably a sufficient barrier to hybridisation over much of their distribution.

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